SEMIOCHEMICALS AND IMPROVEMENTS IN RODENT CONTROL

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ABSTRACT Semiochemicals typically contain sulfur. Here, we present the thesis that sulfurous odors are central to the biological importance of semiochemicals in feeding contexts because they are generated during protein digestion, and hence, provide information about diet composition of donor animals. This information about diet could explain attractiveness of sulfur to carnivores and omnivores, and its repellency to herbivores.

INTRODUCTION

Limited data are available that document economic losses caused by vertebrates (Salmon, 1980). Nevertheless, it is generally recognized that rats (e.g., *Rattus norvegicus*, *Rattus rattus*), other rodents such as mice (e.g., *Mus musculus*, *Peromyscus maniculatus*), and voles (e.g., *Pitymys pinetorum*, *Microtus pennsylvanicus*), lagomorphs (e.g., *Sylvilagus floridanus*), coyotes (*Canis latrans*) and some ungulates (e.g., *Odocoileus virginianus*) cause considerable economic harm (Brooks et al., 1990). In particular, agricultural losses are believed to be substantial (Marsh, 1988), and damage is likely to increase in the future as conservation tillage practices become more widespread (Castrale, 1987). In addition to crop damage, commensal rodents and other pest species undermine and weaken structures (Timm, 1982; Marsh, 1988), and chew through electrical and telephone cables. They also serve as primary reservoirs or hosts to vectors for human and livestock diseases, including viral zoonoses (e.g., equine encephalitis), rickettsial diseases (e.g., Rocky Mountain spotted fever), and bacterial diseases (e.g., salmonella [Gratz, 1988]).

Pest problems can be alleviated through an effective management program based on an understanding of a pest species' biology. In the past, recommendations for control were focused on factors such as species distribution, reproduction, and development, physical attributes of the pests, and population dynamics (Howard and Marsh, 1974; Fall, 1977; Pratt et al., 1977).

More recently, research efforts also have focused on behavioral defenses of pests against dietary poisoning, and on semiochemical influences on feeding.

The term 'semiochemical' has been variously defined in the literature. In the present discussion, semiochemicals are substances that provide biologically important information both intraspecifically and interspecifically. Depending upon the context of presentation, these substances can be attractant or repellent. Because the effects of semiochemicals are typically robust, they can be used to circumvent behavioral defenses against dietary poisoning to enhance pest management.

Three defenses against dietary poisoning are commonly described in the literature: neophobia (that is, avoidance of a new food or flavor), primary food aversion (that is, unlearned initial avoidance of a particular type of food, usually presumed due to bitter taste), and learned food aversion or bait-shyness (that is, avoidance of a particular food following its association with post-ingestional illness, e.g., Reidinger and Mason, 1983).

Attractants

For carnivores (such as coyotes) and for omnivores (such as rats and mice), most attractant semiochemicals are sulfur-containing. This is especially (if not exclusively) true in feeding contexts. The converse is generally true for herbivores, i.e., sulfurous materials are typically feeding deterrents. Illustrative examples are provided below.

When faced with a choice among feeding sites, Norway rats prefer locations that conspecifics are exploiting (Galef and Clark, 1971; Galef and Heiber, 1976). When faced with a choice among several novel foods, naive (observer) rats choose novel foods that have previously been ingested by conspecifics (demonstrators) with whom they have interacted (e.g., Strupp and Levitsky, 1984). This socially mediated transfer of food preference has been observed even when demonstrators are anesthetized and wire-mesh barriers are placed between demonstrators and observers (Galef and Wigmore, 1983). Such findings and the results of other experiments (Galef and Stein, 1985) suggest that diet preference and the transfer of diet preference is mediated in part by volatile chemical cues.

Important volatile information could be the smell of food that a demonstrator has ingested before interacting with an observer. Alternatively, transmission might require a combination of the smell of the ingested diet, and some endogenous (demonstrator-derived) volatile. In a series of experiments designed to test these possibilities, Galef et al. (1985), and Galef and Stein (1985) showed that both the smell of ingested diet and demonstrator-produced volatile signals provided important information.   Demonstrator-produced volatiles were investigated in a series of gas-chromatographic/mass spectroscopic experiments. In these investigations, Galef et al. (1988) found that carbon disulfide and carbonyl sulfide were present on the breath of rats. A

typical reconstructed ion chromatogram showing the elution of carbon disulfide and carbonyl sulfide is provided in Figure 1. The elution of carbonyl sulfide is indicated by the maximum in the mass chromatogram of m/z 60 (molecular ion of carbonyl sulfide), while the elution of carbon disulfide is indicated by the maximum in the mass chromatogram of m/z 76 (molecular ion for carbon disulfide). The spectra for the compounds have been inserted into the figure; both are extremely simple. The spectrum for carbon disulfide consists mainly of the molecular ion m/z 76, the sulfur-containing isotope ion at m/z 78, as well as a small fragment ion at m/z 64. The spectrum of carbonyl sulfide consists primarily of its molecular ion at m/z 60, and an isotope ion at m/z 62.
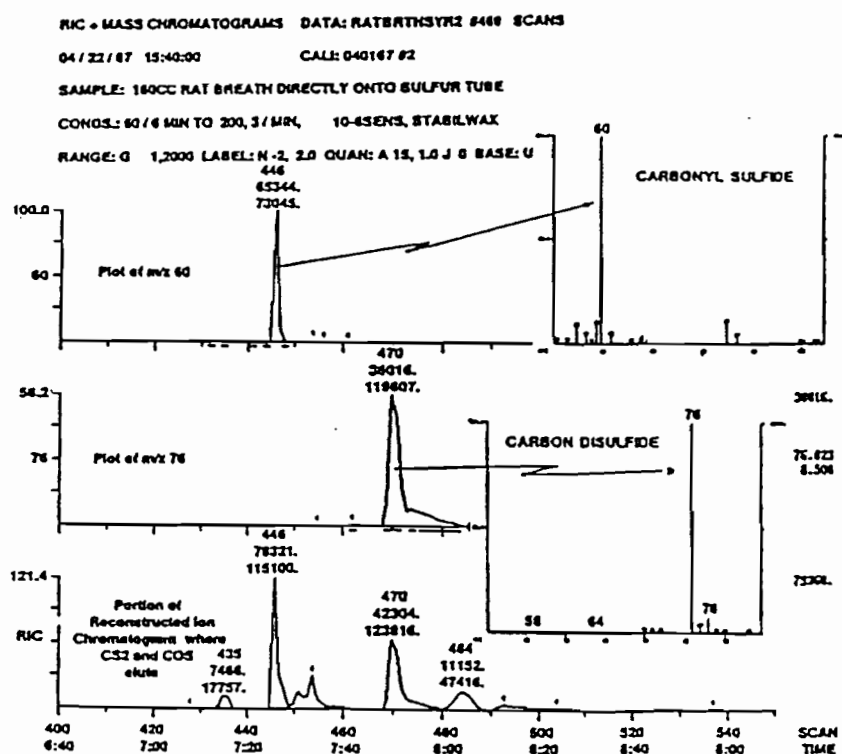

Figure 1. Reconstructed ion chromatograms of rat breath showing molecular ions for carbonyl sulfide and carbon disulfide. The spectrum for carbon disulfide consists mainly of the molecular ion m/z 76, the sulfur-containing isotope ion at m/z 78 as well as a small fragment ion at m/z 64. The spectrum for carbonyl sulfide consists primarily of its molecular ion at m/z 60, and an isotope ion at m/z 62. (From: Galef, B. G., J. R. Mason, G. Preti, and N. J. Bean. 1988. Carbon disulfide: a semiochemical mediating socially-induced diet choice in rats. Physiol. Behav. 42: 1119-1124).

Subsequent experiments with standard amounts of carbon disulfide and carbonyl sulfide permitted calculation of the carbon disulfide and carbonyl sulfide concentrations on breath, as well as retention times for the compounds. The concentrations varied from 1-10 parts per million. The finding that carbon disulfide and carbonyl sulfide are present on the breath of rats is not, in itself, proof that either substance is a semiochemical. For that reason, a series of behavioral experiments were performed. Because carbonyl sulfide is a gas at room temperature and pressure, only carbon disulfide (liquid at room temperature) was examined. When carbon disulfide on cotton batting was associated with novel cocoa or cinnamon odor, it elicited transfer of diet preference to cocoa or cinnamon similar to that produced by exposure to a live demonstrator (Galef et al., 1988). Observers that experienced diet in association with carbon disulfide, like observers that experienced diet smeared on the head of a demonstrator, subsequently exhibited a preference for that diet. However, animals simply experiencing a diet without simultaneous exposure to carbon disulfide did not exhibit a preference for it (Figure 2).
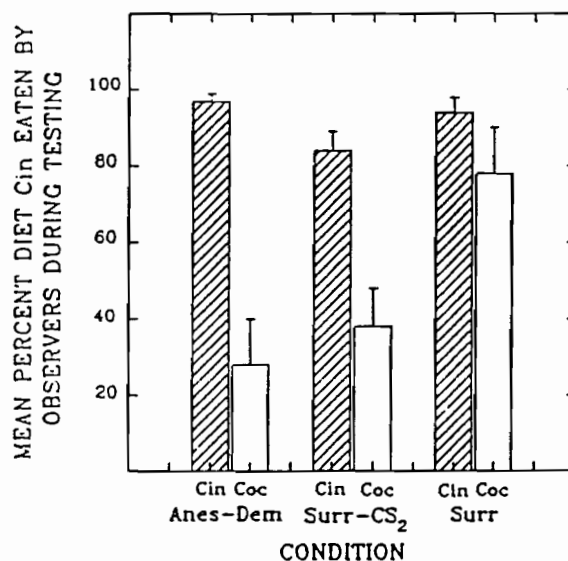

Figure 2. Mean amount of cinnamon (Cin) diet eaten as a percentage of total consumption by rats presented with Cin or cocoa (Coc) flavored diet in conjunction with an anesthetized demonstrator rat (left), cotton batting and carbon disulfide (middle) or batting alone (right). (From: Galef, B. G., J. R. Mason, G. Preti, and N. J. Bean. 1988. Carbon disulfide: a semiochemical mediating socially-induced diet choice in rats. Physiol. Behav. 42: 1119-1124).

Subsequently, carbon disulfide was shown to attract mice as well as rats. In a laboratory experiment (Bean et al., 1988), aqueous solutions of 0.001, 0.01, 0.1, 1.0, and 10.0 ppm carbon disulfide were applied to food pellets. The pellets were weighed and placed in one of two bait enclosures in an open field (Figure 3). The other enclosure contained either plain pellets or pellets scented with butanol. Individual, food deprived mice were then placed in the field and observed for 20 minutes. Photoelectric circuits recorded entries and departures from each bait enclosure. At the end of the observation period, the mice were removed from the field and then consumption was recorded.

Any carbon disulfide concentration enhanced consumption, as well as the investigation of treated areas (Figure 4). Higher concentrations were more effective than were lower concentrations. The most obvious practical implication of these findings is that carbon disulfide may enhance the effectiveness of rodenticide bait formulations by increasing consumption and decreasing neophobia. In addition, because carbon disulfide increases entries into areas where it is present, this odor might improve the effectiveness of traps and tracking powders by increasing investigation of these devices and materials.
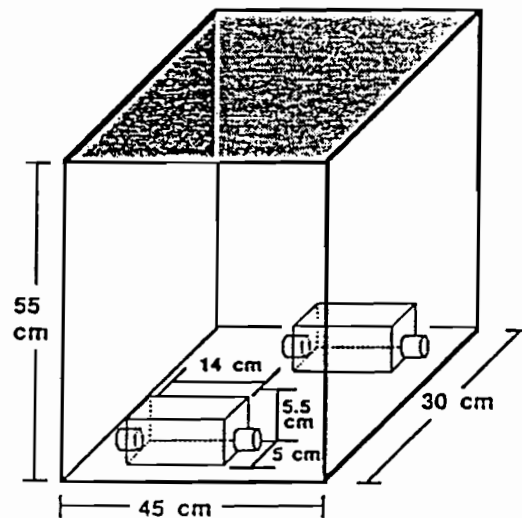

Figure 3. Diagram of open field testing apparatus and bait enclosures used to test carbon disulfide attractiveness to mice. At the beginning of a trial, a mouse was placed through the open top into the center of the apparatus, equidistant from the two enclosures. (From: Bean, N. J., B. G. Galef, and J. R. Mason. 1988. The effect of carbon disulfide on food consumption by house mice. J. Wildl. Manage. 52: 502-507).
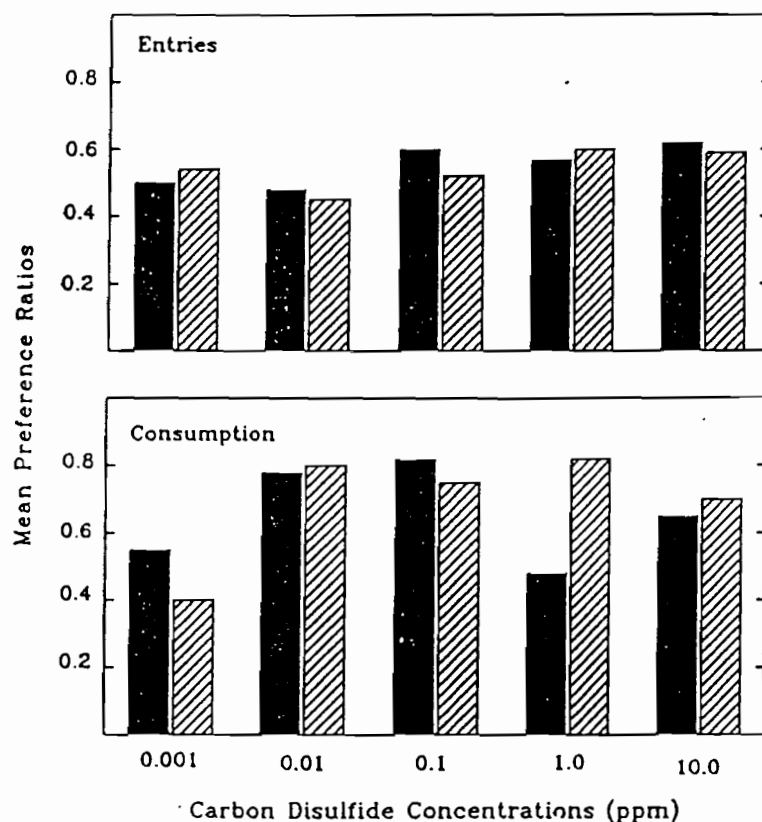
Figure 4. Entries by mice into enclosures and consumption of feed expressed as preference ratios [carbon disulfide entries or consumption divided by total (carbon disulfide and control) entries or consumption]. A ratio of 1.0 indicates total preference for carbon disulfide, 0.5, indifference, and 0.0, total rejection. In each case, carbon disulfide was preferred. (From: Bean, N. J., B. G. Galef, and J. R. Mason. 1988. The effect of carbon disulfide on food consumption by house mice. J. Wildl. Manage. 52: 502-507).

Carbon disulfide could enhance the efficacy of poison baits in a variety of ways beyond increasing intake and investigation times. Results of several experiments (Galef, 1986a and b) indicate that the experience of the smell of a diet, either on the breath of a conspecific or in association with carbon disulfide interferes with Norway rats' ability to learn food aversions to that diet. Thus, carbon disulfide could both increase bait consumption and, by interfering with

acquisition of bait shyness, increase the probability that an individual eating a sublethal dose of bait during an initial feeding bout would subsequently return to consume a lethal dose.

The utility of carbon disulfide as a practical rodent attractant has not been systematically evaluated. However, there are field data consistent with the notion that carbon disulfide can increase visits to bait stations and encourage bait consumption (Mason et al., 1988). In order to perform this field test, we selected several sites near Poughkeepsie, New York with large Norway rat populations. Bait stations were constructed from pairs of 50 cm long x 10 cm diameter sections of PVC pipe and then placed at each site (Figure 5). The pipes were attached side-by-side with wire. One end of each pipe was open, while the other was closed with a removable PVC cap. Wire was used to attach bait blocks inside each cap.
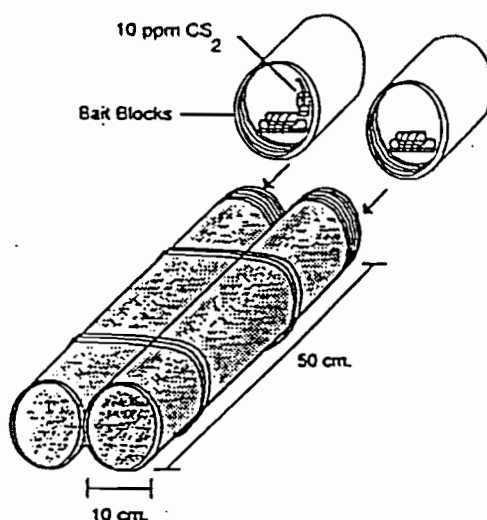

Figure 5. Illustration of device used to present carbon disulfide and bait to free-ranging Norway rats. (From: Mason, J. R., N. J. Bean and B. G. Galef. 1988. Attractiveness of carbon disulfide to wild Norway rats. Proc. Vertebr. Pest Conf. 13: 95-97).

The only difference between the pipes in each pair was that one pipe also contained a vial filled with 10 ml of 10 ppm carbon disulfide solution. This solution was prepared by diluting reagent grade carbon disulfide in distilled water, and agitating for approximately 30 minutes. Vials were attached to the PVC cap immediately above the bait blocks, and were fitted with cotton wicks that protruded 2-cm from/their caps.

Three locations were randomly selected at each of the test sites, with the qualification that the locations were at least 15 meters apart. Over 6 days, a bait

station was placed at each location at each site twice. For all 6 tests at each site, bait stations were set out at approximately 1700 hrs, and retrieved at 0900 hrs of the following day. The pipe in each pair that contained carbon disulfide was counterbalanced across tests, and total consumption (g) of bait on each test night was recorded.

The results showed that consumption of bait blocks paired with carbon disulfide was three times higher than consumption of plain blocks (Figure 6).
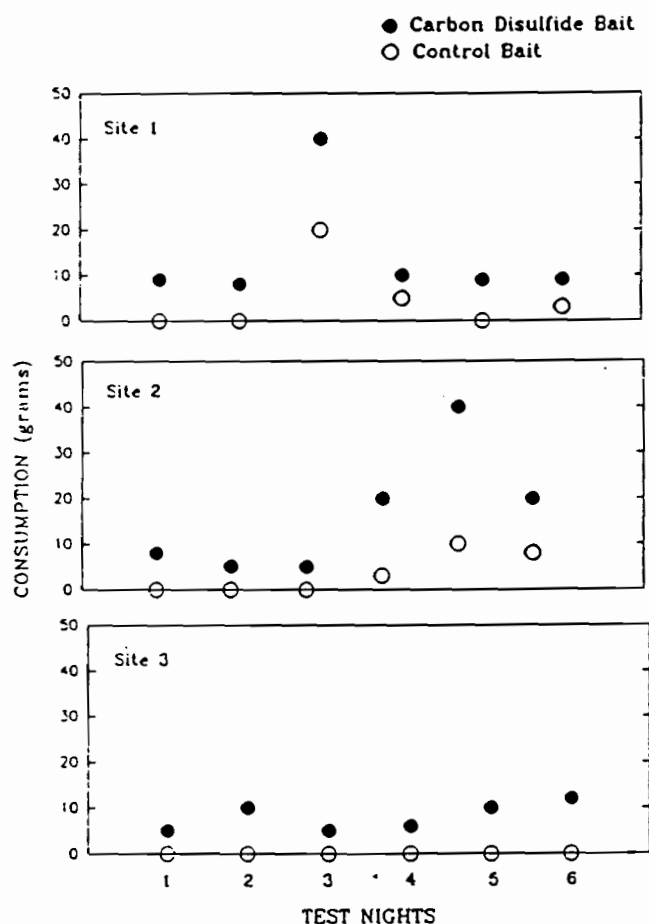

Figure 6. Consumption of carbon disulfide adulterated bait and control bait by free-ranging Norway rats. (From: Mason, J. R., N. J. Bean, and B. G. Galef. 1988. Attractiveness of carbon disulfide to wild Norway rats. Proc. Vertebr. Pest Conf. 13: 95-97).

Moreover, inspection of nightly test results suggests that overall consumption increased during the course of the assessment. This increase could reflect diminishing neophobia to the bait stations. Interestingly, however, even

on the first night, carbon disulfide enhanced consumption. This enhanced consumption even during the initial exposure of bait is consistent with laboratory results demonstrating that carbon disulfide decreases neophobia.

Carbon disulfide is attractive not only to omnivores such as rats and mice, but also to carnivores like dogs and cats. Other sulfurous odors also are attractive. Garlic odor (diallyl disulfide) is a flavor additive to both dog and cat foods (D. Passe, personal communication), and both it and onion odor (propane thiosulfinate) enhance consumption by these animals (Figure 7, Mason, unpubl. obs.). Since successful coyote (*Canis latrans*) lure formulations always contain sulfurous odorants (G. Preti, unpublished), it seems certain that sulfurous compounds are attractive to these wild canids as well.
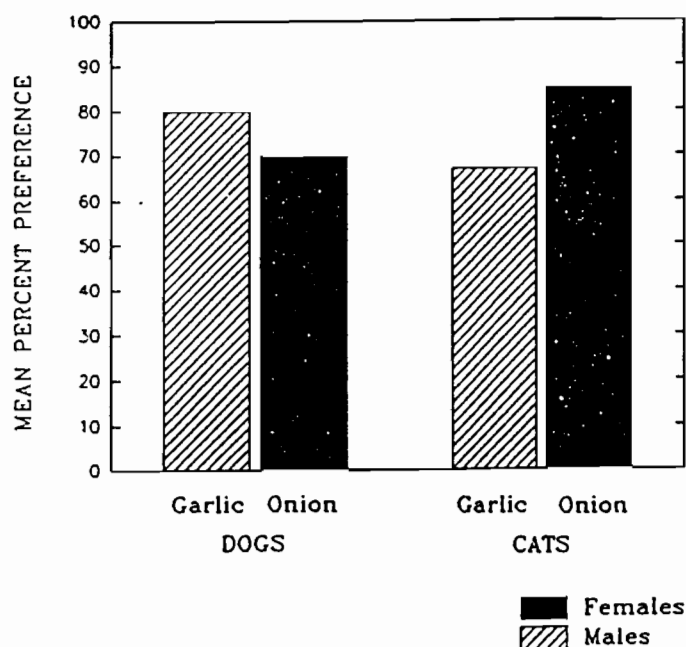

Figure 7. Preferences shown by dogs and cats for garlic and onion extract presented in dry chow in 2-bowl tests. The alternative in each case was plain dry chow.

Repellents

Anecdotal and experimental evidence support the view that sulfur-containing compounds are repellent to herbivores. Grazing ungulates, such as mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*); herbivorous rodents like mountain beaver (*Aplodontia rufa*), and lagomorphs like cotton-tailed rabbits (*Sylvilagus floridanus*) are repelled by Big Game Repellent (BGR) (Campbell, pers. commun.; Conover, 1987; Conover and Kania, 1987; DeVoe and Schaap, 1987), a complex mixture of sulfurous materials that, incidentally, is attractive to coyotes (Bullard pers. commun.).

The omnivore-carnivore/herbivore difference in response to sulfur compounds may span across Classes (Aves and Mammalia). Among birds, there is evidence that carnivores (e.g., turkey vultures, *Cathartes aura*) not only find food on the basis of sulfur containing volatiles (Stager, 1967; Houston, 1986), but also reject meat on the basis of sulfurous compounds from carcasses that have rotted (Houston, 1986). Conversely, herbivorous species (e.g., Canada geese, *Branta canadensis*) avoid plants such as wild onion (Mason, unpubl. obs.), perhaps because these plants exude sulfur-containing odorants (such as S-propyl propane thiosulfinate).

The available evidence suggests that the repellency of sulfur odors to herbivores is mediated, in part, by volatility. Thus, when the repellency of C_2-C_8 dialkyl disulfides to free-ranging white-tailed deer (*Odocoileus virginianus*) was examined in a field test, avoidance was negatively correlated with carbon chain-length (Figure 8).
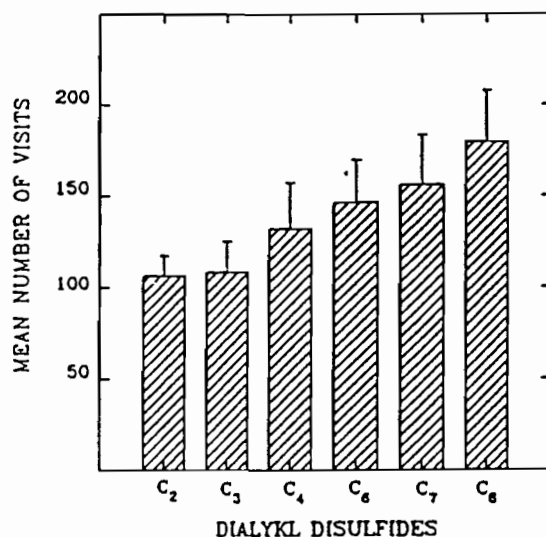

Figure 8. Mean numbers of visits/week by deer to bait sites scented with dialkyl disulfides. The mean number of pretreatment visits to all sites was equivalent to the number of visits to C_8 (octyl disulfide). Repellency appears to be positively associated with volatility.

Degree of volatility alone does not, however, provide a full explanation for the repellency of sulfur compounds to herbivores. Odor quality also appears to be important. For example, dimethyl disulfide, dimethyl trisulfide, and dimethyl tetrasulfide have been identified in lion (*Panthera leo*) dung, a 'universal' deer repellent (Abbott et al., 1990). While these sulfur compounds

presented alone or in combination are repellent, they are not as effective as is lion dung itself.

Several recent studies in our laboratory have shown that odor cues from a number of predators reduce feeding in mountain beavers (*Aplodontia rufa*), when the odors are presented in the immediate vicinity of a food source (Epple et al., 1993). Specifically, mountain beavers were offered food from 2 bowls, one scented with a predator-derived odor, and the other with a control odor. The food itself remained untainted. Anal gland secretion from American mink (*Mustela vison*), and urine from mink, bobcat (*Lynx rufus*), coyote, and domestic dog were used as predator odors, while butyric acid and urine from prairie voles (*Microtus ochrogaster*) served as control scents. All of the predator odors significantly reduced consumption of diced apple in 2 hour tests relative to the control odors (Figure 9). Subsequent experiments showed that their repellent effects can last over several days.
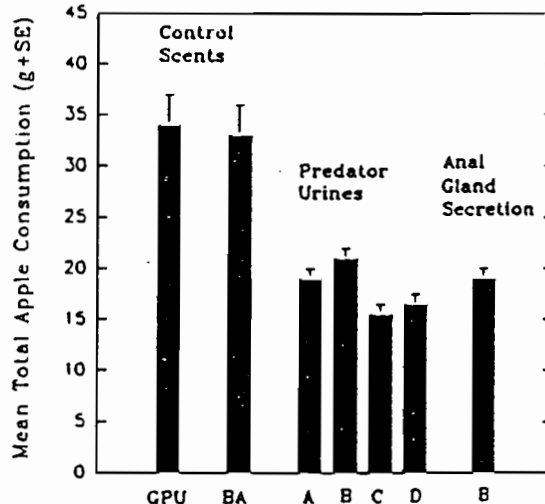

Figure 9. Mean consumption of apple paired with control odors, predator odors, or mink anal gland secretion by mountain beaver. Abbreviations: GPU = guinea pig urine, BA = butyric acid, A = dog, B = mink, C = bobcat, D = coyote. (From: Epple, G., J. R. Mason, D. L. Nolte, and D. L. Campbell, 1993, Effects of predator odors on feeding in the mountain beaver (Aplodontia rufa). J. Mammal., in press).

Thus, when mountain beavers were offered their regular chow continuously for 5 days from bowls scented with coyote urine or water, avoidance of the urine scented bowl remained strong (Figure 10).

In another study, mountain beavers were offered choices among Douglas fir (*Pseudotsuga menziesii*) seedlings which had been immersed in coyote urine,

mink urine, a 1% solution of ortho-aminoacetophenone (mouse repellent, Nolte et al., 1993), a 1% solution of denatonium benzoate, an extremely bitter compound (Budavari et al., 1989), or water. The seedlings were available for 2 weeks. Both predator urines reduced browsing on Douglas fir seedlings, relative to the water control, while the other substances showed no repellent effects (Figure 11). An experiment with salal (*Galtheria shallon*) instead of Douglas fir produced similar effects, although both denatonium benzoate and ortho-aminoacetophenone were moderately effective in preventing grazing on salal.
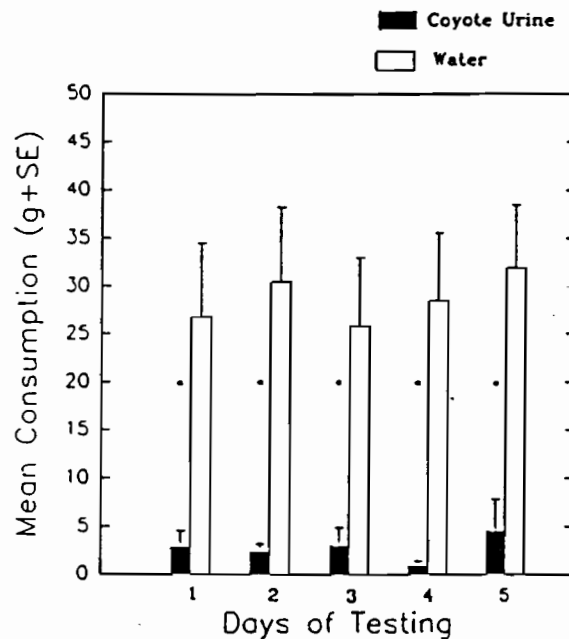

Figure 10. Mean consumption of dry chow throughout 5 days of testing from feeding stations scented with coyote urine or water. (From: Epple, G., J. R. Mason, D. L. Nolte, and D. L. Campbell, 1993. Effects of predator odors on feeding in the mountain beaver (Aplodontia rufa). J. Mammal., in press).

Studies on a number of other mammals, including lagomorphs, rodents, and ungulates also have documented the effectiveness of predator-derived chemical cues in promoting avoidance. A number of experiments have demonstrated the effects of predator feces, urine, and glandular secretions on spacing, exploitation of food resources and damage to plants in some old world and new world Lagomorpha (Sullivan et al., 1985a; Sullivan and Crump, 1984 and 1986a; Robinson, 1990), in several species of *Microtus* (Stoddart, 1976, 1980, 1982; Dickman and Doncaster, 1984; Gorman, 1984; Sullivan and Crump, 1986b; Sullivan et al., 1988a and b, 1990a; Robinson, 1990), in woodchucks (*Marmota monax*, Swihart, 1991), and in Norway rats (Vernet-Maury, 1980; Vernet-Maury et al., 1984). Extensive laboratory and field studies by Sullivan and co-workers, testing a number of synthetic components of

predator scent, resulted in a potential new rodent repellent comprised from two constituents of mustelid anal gland secretion (Sullivan and Crump, 1986a and 1986b; Sullivan et al., 1988a, 1988b, 1990a; 1990b; Merkens et al., 1991). Both of these secretions are sulfur-containing.
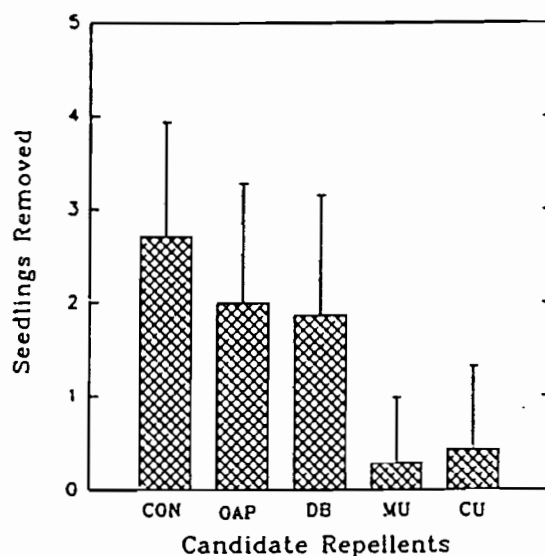

Figure 11. Mean number of Douglas fir seedlings clipped by mountain beaver in a 2 week trial. Prior to testing, the seedlings were soaked in water (CON), ortho-aminoacetophenone (OAP), denatonium benzoate (DB), mink urine (MU), or coyote urine (CU). (From: Nolte, D. L., J. P. Farley, D. L. Campbell, G. Epple, and J. R. Mason. Potential repellents to prevent mountain beaver damage. Submitted for publication).

Fecal material and urine from a variety of carnivores reduce feeding in ungulates, including roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), black-tailed deer (*Odocoileus hemionus columbianus*), white-tailed deer and domestic sheep and cattle (Van Haaften, 1963; Müller-Schwarze, 1972; Melchiors and Leslie, 1985; Sullivan et al., 1985b; Abbott et al., 1990; Pfister et al., 1990; Swihart et al., 1991; Weldon, 1990). Very slow habituation to predator derived chemical cues was evident in several of these studies (Sullivan and Crump, 1984; Sullivan et al., 1988a; Swihart, 1991).

Although the repellency of predator odors is influenced by both habitat characteristics (Merkens et al., 1991), and other ecological factors (Swihart et al., 1991), there is suggestive evidence that avoidance of repellents by pests is due largely to the presence of a few key chemical cues. The responsiveness of many prey species to chemical cues from allopatric predators supports this notion. As we stated earlier, mountain beavers avoid feeding from bowls

scented with mink (*Mustela vison*) anal gland secretion, or with urine from mink, coyote, bobcat, but also from bowls scented with urine from domestic dogs. Similarly, other herbivores are repelled by chemical cues from carnivores that do not normally prey upon them. European *Microtus agrestis* avoid traps scented with weasel (*Mustela nivalis*) anal gland secretion, but also traps scented with jaguar (*Panthera onca*) or tiger (*Panthera tigris*) urine (Stoddart, 1976, 1980, 1982). Orkney voles (*Microtus orcadensis*) avoid urine from the stoat (*Mustela erminea*), a predator from which voles on the island have been separated for a considerable part of their evolutionary history (Gorman, 1984). Dickman and Doncaster (1984) report that small rodents avoid scent from badger (*Taxidea taxus*), a species absent from their study area.

European roe deer and red deer and American black-tailed deer show feeding inhibition in response to fecal chemical cues derived from African lions, snow leopards (*Panthera unca*), and tigers (Abbott et al., 1990; Müller-Schwarze, 1972; van Haaften, 1963). Indeed, Abbott et al. (1990) recently prepared an organic solvent extract from lion feces, and synthetic formulations of compounds found in lion feces that are as effective as the total fecal material in reducing feeding by European red deer.

Although mammals respond to scents from allopatric predators (and often are repelled by them), chemical cues from sympatric species are often more effective. Black-tailed deer show strong avoidance of food scented with fecal material from cougar (*Felis concolor*) and coyote, while fecal odors from lion, leopard, and tiger are less effective (Müller-Schwarze, 1972 and 1983). Bobcat and coyote urine reduce browsing by white-tailed deer, with bobcat urine being more effective than coyote urine, while human urine has little effect (Swihart et al., 1991). In contrast, Sullivan et al. (1985b) found that black-tailed deer are more repelled by coyote than by bobcat urine.

The responses to chemical cues from allopatric predators and the failure to habituate to predator odors have been interpreted as evidence that responses to these stimuli are innate (Stoddart, 1980; Dickman and Doncaster, 1984; Müller-Schwarze, 1972; Robinson, 1990). This notion is supported by the responses of hand-raised, predator-naive deer to carnivore dung (Müller-Schwarze, 1972), and by responses of *Microtus* species, living on the predator-free island of Orkney to chemical cues from stoat (Gorman, 1984).

CONCLUSIONS

Semiochemicals in the context of feeding, whether attractive or repellent, are usually (if not always) sulfur-containing. In part, the effectiveness of these cues is related to volatility; more volatile stimuli are more powerful stimuli. But volatility alone does not explain why sulfur-containing odors should be important relative to other equally volatile stimuli. We speculate that sulfur-containing odorants are important because they reflect protein digestion. Protein

digestion, in turn reflects diet. Hence, the attraction of sulfur odors to carnivores and omnivores, and their repellency to herbivores. Because the odors are digestive by-products, breath and other excreta such as feces and urine probably contain them. At present, we are attempting to test the importance of diet for the production of sulfur-containing semiochemicals by feeding coyotes either meat or vegetable diets, and then collecting urine samples from the two groups. These samples are then being presented to mountain beavers. Our hypothesis is that the urine from meat-eating coyotes will repel the beavers, while urine from animals fed vegetables will not. Whatever the results of these experiments, sulfur-containing odorants show promise as components of integrated pest management programs. From this point-of-view, sulfurous odors may be especially useful because the same substance at the same concentration may be both attractant and repellent, depending upon the species under consideration.

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